

# Tidal movements and residency of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) in an Oregon salt marsh channel

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**Abstract:** A novel application of full-duplex passive integrated transponder (PIT) tag technology was used to investigate movements of individual subyearling Chinook salmon (*Oncorhynchus tshawytscha*; fork length  $\geq 60$  mm) into and out of tidally flooded salt marsh habitat in the Salmon River estuary, Oregon, USA. PIT interrogation was effective, with mean tag detection  $\geq 92\%$ . Salmon movement peaked late during both flood and ebb tide periods, indicating that salmon did not drift passively. Most movements were in the direction of tidal currents, but 20% of individuals entered the channel against the ebbing tide. Individuals occupied the intertidal channel for a median 4.9 h and as long as 8.9 h per tidal cycle, and few were detected moving when water depth was  $<0.4$  m. Some individuals used the channel on multiple successive tidal cycles, and others entered intermittently over periods of up to 109 days. Using an individual-based approach, we characterized diversity of juvenile Chinook salmon behavior within a marsh channel, providing insight into the value of such habitats for conservation and restoration of salmon populations.

**Résumé :** Une utilisation inédite de la technologie des transpondeurs passifs intégrés à transmission bidirectionnelle simultanée (étiquettes PIT) a servi à étudier les déplacements de saumons chinook (*Oncorhynchus tshawytscha*; longueur à la fourche  $\geq 60$  mm) âgés de moins d'un an lors de leur entrée ou sortie d'un habitat de marais salant inondé par la marée dans l'estuaire de la rivière Salmon, Oregon, É.-U. Le système d'interrogation des PIT est efficace avec une détection moyenne de  $\geq 92\%$  des étiquettes. Les déplacements des saumons atteignent un maximum à la fin des marées montantes et descendantes, ce qui indique que les saumons ne dérivent pas passivement. La plupart des déplacements se font dans le sens des courants de marée, mais 20 % des individus pénètrent dans le chenal contre la marée descendante. Les individus se retrouvent dans le chenal intertidal pour une médiane de 4,9 h et jusqu'à 8,9 h pendant un cycle de marée et certains ont été observés se déplacer dans des eaux de  $< 0,4$  m de profondeur. Quelques individus utilisent le chenal pendant plusieurs cycles successifs de marée et d'autres y pénètrent de façon intermittente pendant une période aussi longue que 109 jours. En utilisant une approche basée sur l'individu, nous décrivons la diversité des comportements de jeunes saumons chinook dans un chenal de marais, ce qui fournit une perspective sur la valeur de tels habitats pour la conservation et la restauration des populations de saumons.

[Traduit par la Rédaction]

## Introduction

During their juvenile migration from freshwater to marine habitat, ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) may rear for prolonged periods in subsidiary and blind channel networks that connect mainstem estuarine channels with peripheral wetlands (Congleton et al. 1981; Simenstad 1983; Healey 1991). Such channel networks are often intertidal, necessitating twice-daily evacuation of wetland areas

and redistribution of nekton communities across hundreds of metres of habitat as channels flood and drain with the tide (Rozas 1995; Gibson 2003). Despite obligatory tidal emigrations, mark-recapture experiments indicate that individual Chinook salmon may return to particular wetland channels for days to months, moving into flooded channel networks during high tides and retreating to subtidal habitats during low tides (Congleton et al. 1981; Levy and Northcote 1982; Shreffler et al. 1990).

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The use of tidal channels as salmon rearing habitats has been the subject of multiple studies over the past several decades. Research has emphasized seasonal patterns of salmon abundance (Congleton et al. 1981; Levy and Northcote 1982), salmon feeding habits and prey resources (Shreffler et al. 1992; Gray et al. 2002), and restoration and recovery of habitat function in formerly degraded wetlands (Shreffler et al. 1990; Miller and Simenstad 1997; Gray et al. 2002). Recent work suggests that the presence or condition of estuarine marsh habitat may be linked to life history diversity and hence resilience of salmon populations (Bottom et al. 2005a, 2005b). Understanding the behavior of individual salmon within estuarine wetlands is necessary to evaluate habitat–life history associations and to predict changes to salmon populations that might result from wetland degradation or recovery (Simenstad and Cordell 2000). Yet patterns of salmon movement within and among tidal channels — including the timing and duration of tidal excursions into marsh habitats — remain poorly understood, particularly at fine temporal and spatial scales.

One impediment to studying salmon behavior in tidal marshes has been difficulty in tracking individuals with ocean-type life histories that are most likely to reside in marsh habitat. Because such fish (typically 40–100 mm fork length) are too small to monitor using active radio or acoustic telemetry, active telemetry studies of salmon in estuaries have used larger yearling migrants (e.g., Moser et al. 1991; Miller and Sadro 2003; Schreck et al. 2006) and (or) hatchery-reared fish (Semmens 2008.) The few studies that have described movement of small salmon in intertidal marsh channels have relied on physical recapture of marked fish using seines or traps (Levy and Northcote 1982; Shreffler et al. 1990). Repeated capture and handling may alter fish behavior, however, and such conventional methods are poorly suited to resolving movements that occur over the short time scale of tidal cycles.

We sought to address this problem by using full-duplex (FDX) passive integrated transponder (PIT) tag technology (Prentice et al. 1990a). PIT tags are common tools in freshwater fish research, where detection systems incorporating stationary, in situ PIT antennas have allowed passive monitoring of fish movements at multiple scales in natural and simulated stream habitats (reviewed by Zydlewski et al. 2006). High-salinity water has limited application of PIT detection technology in marine and estuarine habitats by reducing the distance over which PIT tags can be detected (e.g., McCormick and Smith 2004). Adams et al. (2006) and Meynecke et al. (2008), however, both reported using half-duplex (HDX) PIT tag detection systems for monitoring the movement of fish in salinities ranging from 2 to 28 PSU. Both investigators used HDX PIT tags measuring 23.1 mm long  $\times$  3.4 mm in diameter and weighing 0.6 g in air. Such tags (the smallest HDX tags commercially available) are too large and heavy for use with subyearling salmon, but at the time of our study, FDX tags measuring 12.5 mm long  $\times$  2.07 mm in diameter and weighing 0.102 g in air were available. Improvements in the read range of FDX tags and improved performance and capability of the transceiver system (e.g., electromagnetic interference filtering, operation of multiple antennas from a single transceiver, and antenna design) recently have increased the feasibility of using FDX

PIT tag technology with small fish in brackish water habitats.

We operated a stationary FDX PIT tag detector within a blind, tidal salt marsh channel of the Salmon River estuary, Oregon, for several months during the summers of 2004 and 2005, coincident with a conventional mark–recapture experiment in the estuary using FDX PIT tags. Our objectives were to assess the utility of this approach for monitoring movement of small salmon in shallow estuarine habitats, investigate the timing and duration of intertidal channel use by individual age-0 Chinook salmon, identify environmental limits (e.g., temperature, depth) on channel occupancy, and test whether patterns of tidal movement varied among individuals of different sizes or tagging location.

## Materials and methods

### Study area

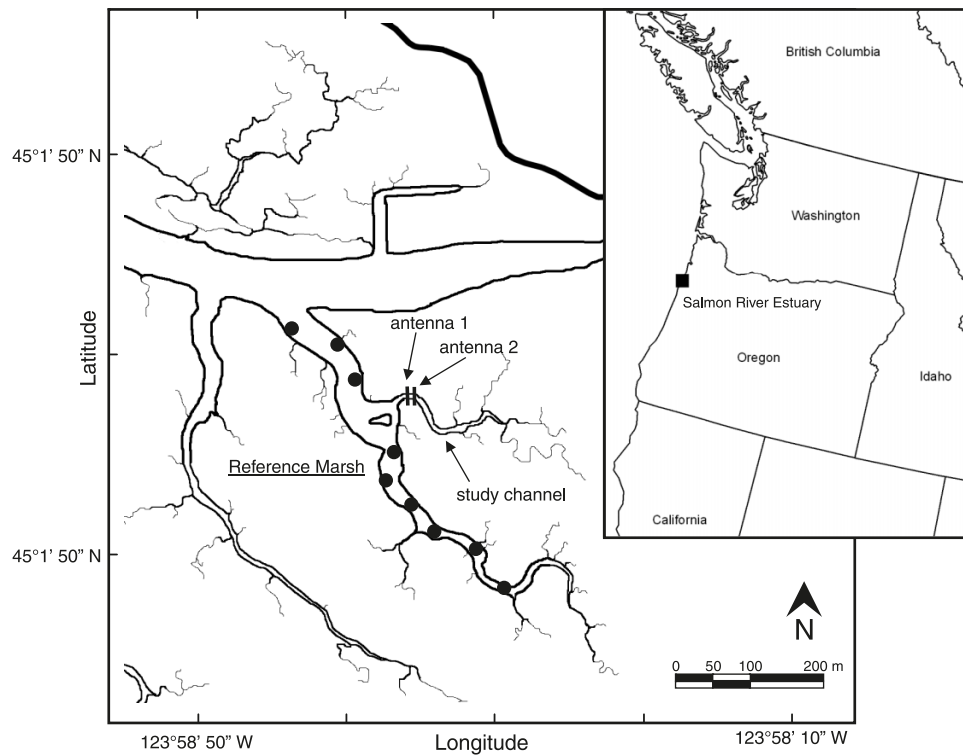
The Salmon River drains a catchment of 194 km<sup>2</sup> in the Oregon, USA, coastal mountains and flows into the Pacific Ocean at Cascade Head (45°01'N, 123°58'W; Fig. 1). The lowest 6.5 river kilometres (rkm) form a tidally influenced estuary, and the area of the estuary between rkm 2.0 and rkm 4.5 includes over 200 ha of salt marsh intersected by tidal marsh channels. Subyearling Chinook salmon are the dominant salmonids in the estuary, typically occurring in marsh channel habitats from March through October, with peak abundance in late spring or early summer. The estuary is the site of a long-term study of salmon rearing in tidal marsh channels (Gray et al. 2002; Bottom et al. 2005a).

Our study channel was a blind, secondary channel within a dendritic network of intertidal channels that joins the mainstem Salmon River at rkm 3.2 (Fig. 1). This larger channel network intersects an 80 ha, mature high salt marsh (Jefferson 1974) previously described as the Salmon River “reference marsh” or “control marsh” (Gray et al. 2002). Surface area of the study channel was approximately 2005 m<sup>2</sup>, comprising 9.5% of the entire reference channel network. Width of the study channel at the detector site was 8 m, and water depth varied from ~1.5 m at high tide to <0.1 m on most summertime low tides. During both 2004 and 2005, high tide surface water salinity in the study channel varied from less than 5 PSU in June to 28–30 PSU in August and September. The water column was often stratified by salinity in late summer.

### Fish tagging

During high tides between 18 May and 6 July 2004, juvenile Chinook salmon were captured by beach seining, PIT tagged, and released at nine sites within the primary channel of the reference marsh ( $N = 671$ ) (Fig. 1). Tagging followed the techniques of Prentice et al. (1990a) using 12.50 mm long  $\times$  2.07 mm FDX PIT tags (model TX1411ST; Digital Angel Corp., St. Paul, Minnesota; weight 0.102 g in air). Prior to tagging, fish were anesthetized in a bath of ambient water from the marsh channel containing  $\leq 50$  mg·L<sup>-1</sup> tricaine methanesulfonate (MS-222). Tags were inserted into the body cavity using a 12-gauge syringe, and tagged fish were allowed to recover from anesthesia in an aerated water bath before their release near the site of capture. Using the same methods, an additional 572 Chinook salmon were

**Fig. 1.** Map of study site in Salmon River estuary (Oregon, USA). Solid circles indicate locations where Chinook salmon (*Oncorhynchus tshawytscha*) were PIT tagged in the reference marsh in 2004 and 2005.



tagged and released at the same reference marsh sites between 28 June and 1 August 2005. Water temperature and salinity during tagging ranged from 9 °C to 19 °C and from 3 PSU to 18 PSU, respectively.

All tagged Chinook salmon were naturally produced (i.e., not spawned in a hatchery) and ranged from 60 to 116 mm fork length at the time of tagging. Previous studies have shown that PIT tagging has a minimal effect on survival, growth, and performance of salmonids of this size and larger (Prentice et al. 1990b; Ombredane et al. 1998; Newby et al. 2007). Tag weight ranged from 0.8% to 5.4% of body weight (median 3%). Brown et al. (2006) detected no effect on growth or swimming speed of juvenile Chinook salmon implanted with transmitters between 3.1% and 10.7% of body weight.

#### Detection equipment and data collection

In 2004, the PIT tag detection system consisted of a single 24V FS-1001A transceiver (Digital Angel Corp.) powered by four 12V batteries and connected to one antenna anchored in the tidal channel. A Palm M130 handheld computer (Palm Inc., Sunnyvale, California) connected to the transceiver's serial port recorded time, date, and tag code information for each tag detection and periodically logged the transceiver's current, phase, and noise level using the program FS1001 v1.1 (Oregon RFID, Portland, Oregon).

In 2005, we replaced the FS-1001A transceiver with a newer model FS-1001M transceiver (Digital Angel Corp.). The FS-1001M was capable of multiplexing — operating up to six antennas by sequentially switching power to each antenna several times per second. To the new multiplexing transceiver, we attached the same antenna used in 2004

(antenna 1) and an additional antenna (antenna 2) anchored approximately 20 m farther into the study channel (Fig. 1). The two antennas enabled direction of fish movement to be determined via the time and date recorded with each tag detection. The FS-1001M transceiver was capable of tuning the antenna fields dynamically (automatic tuning) to maximize tag read distance. This feature resulted in improved tag detection efficiency across tidally and seasonally variable water depth and salinity. During 2005, tag detection and transceiver diagnostic data were logged with a Dell Axim handheld computer (Dell Inc., Round Rock, Texas) using the program MiniMon v1.4 (Pacific States Marine Fisheries Commission).

During both years, the transceiver, batteries, and data logger were contained within a 1 m × 1 m × 0.5 m stainless steel box anchored on the marsh surface above maximum high tide elevation. Batteries were exchanged weekly and recharged onshore.

Both antennas originally were designed and constructed by Digital Angel Corp. to detect PIT-tagged adult fish passage at McNary Dam on the Columbia River (Muir et al. 2001). Each antenna consisted of a continuous length of 14 AWG Teflon coated wire wrapped 13 times into a 170 cm × 64 cm rectangular coil. A “shield” of 24 cm wide, 6 mm thick, sheet aluminum channel surrounded the exterior of the wire coil with approximately 10 cm of open space between the shield and the coil on all sides. Both the antenna coil and aluminum shield were housed within an air-filled watertight housing of 18 cm × 27 cm fiberglass (antenna 1) or welded plastic (antenna 2) box channel. The inside dimension of these rectangular housings (i.e., the area that fish passed through to be detected) measured 50 cm × 157 cm (0.78 m<sup>2</sup>) on each antenna. Laboratory testing using



**Fig. 2.** Antenna 1 installed in study channel at a moderately low tide.



FS-1001 transceivers under RF noise conditions similar to the Salmon River study site indicated that these antennas detected model TX1411ST PIT tags when the transceiver current was as low as 1.9 A.

We attached each antenna to two wooden posts driven into the marsh channel substrate, with the long axes of the antennas oriented vertically and located so that the antenna openings were centered on the thalweg of the tidal channel. Nets (0.5 cm mesh) extended from the wooden posts to the shoreline both above and below the antennas to direct fish through the antenna openings (Fig. 2).

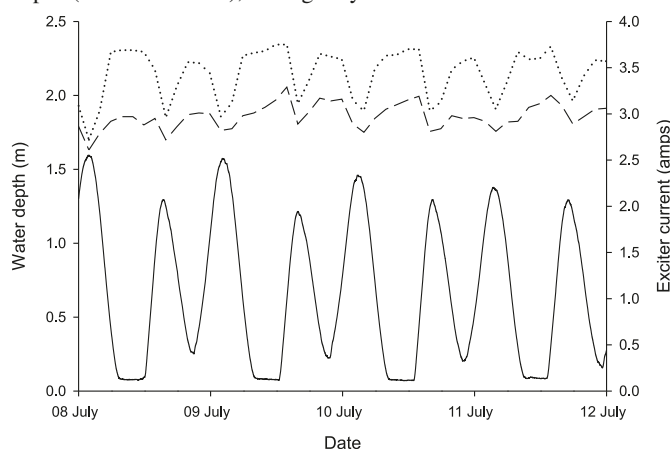
In 2004, we operated the detector system from 15 June to 10 July and from 18 August to 21 October. We removed the nets in mid-July to avoid interfering with an ongoing long-term fish trapping study in the study channel. In 2005, the detector operated continuously from 28 June through 12 September, except for five days when the transceiver shut down due to low battery power.

During 2004, we monitored water temperature at the detector site with a HOBO temperature logger (model H8; Onset Computer Corp., Bourne, Massachusetts). In 2005, we monitored both water temperature and depth with a data logger positioned on the channel bottom between the two antennas (HOBO model U-20-001-01; Onset Computer Corp.). Salinity at the water surface and within the water column was recorded at least twice a week during both years using a handheld refractometer or electronic salinity meter (YSI, Inc.).

### Detection efficiency

Periodically during high tides, we verified the ability of the detection system to recognize PIT tags by passing test tags taped to a stick through the center of each antenna. Twice in 2004 and five times in 2005, we also released groups of tagged salmon into the study channel above the detector system during high tides to test the efficiency with which the nets and antennas combined to detect tagged fish moving out of the study channel. Twenty-seven such “efficiency fish” were released in 2004 and 76 were released in 2005.

**Fig. 3.** Exciter current of antenna 1 (dotted line) and antenna 2 (broken line) across a typical series of tides, indicated by water depth (continuous line), during July 2005.



Efficiency testing was based on the assumption that all fish released above the antennas would leave the channel as it dewatered on the ebbing tide. Accordingly, we defined detection efficiency as the percentage of each group of efficiency fish detected on the first ebbing tide after release. Because efficiency fish released in 2005 must have passed antenna 2 to reach antenna 1, the efficiency with which antenna 2 detected fish exiting the study channel was defined as the percentage of efficiency fish detected on antenna 1 that were also detected on antenna 2. Similarly, fish that were tagged and released outside of the study channel (i.e., in the adjacent, higher-order reference channel; Fig. 1), subsequently moved into the channel volitionally, and were detected on antenna 2 provided a means to evaluate the efficiency with which antenna 1 detected fish entering the study channel. We could not independently assess the efficiency with which antenna 2 detected incoming fish, but we have no reason to believe that it would differ substantially from the outgoing efficiency.

## Results

### Performance of detection equipment

Brackish water flooding increased the electrical load on antennas and caused transceiver current to vary tidally, decreasing as the amount of water in the channel increased (Fig. 3). Transceiver current ranged from 2.4 to 6.2 A but never dropped below the 1.9 A threshold of tag detection, even when salinity was highest during late summer. Water depth accounted for a large proportion of the observed variation in current for each antenna (linear regression of transceiver current on water depth in 2005,  $r^2 = 0.93$  for antenna 1,  $r^2 = 0.70$  for antenna 2;  $p < 0.0001$ ). Test tags passed manually through the center of the antenna fields during high tides confirmed that both antennas maintained sufficient electromagnetic field strength to detect tags throughout the tidal cycle at surface water salinity as high as 29 PSU.

Detection rate of tagged efficiency fish exiting the channel ranged from 69% to 100% (mean 92%; Table 1). During the two tests with efficiencies lower than 90%, efficiency fish had been distributed particularly high in the study chan-

**Table 1.** Detection efficiency of tagged Chinook salmon (*Oncorhynchus tshawytscha*) released into study channel at high tide (i.e., efficiency fish).

Date	Number released	Number detected				Efficiency (%)		
		Both antennas	Antenna 1 only	Antenna 2 only	Not detected	Antenna 1	Antenna 2	Overall
18 August 2004	13	na	9	na	4	69	na	69
16 September 2004	14	na	14	na		100	na	100
30 June 2005	31	13	8	5	5	68	62	84
7 July 2005	10	10				100	100	100
13 July 2005	12	11	1			100	92	100
20 July 2005	13	12			1	92	100	92
1 August 2005	10	9	1			100	90	100
Mean						90	89	92

**Table 2.** Summary of Chinook salmon (*Oncorhynchus tshawytscha*) tagged and released in Salmon River estuary outside of study channel and subsequently detected by PIT antenna during 2004 and 2005.

Tagging dates	Individuals tagged	Total detections	Individuals detected	% detected	Time-at-large	
					Median (days)	Maximum (days)
18 May – 6 July 2004	697	493	123	18	16	128
28 June – 1 August 2005	572	369	75	15	9.5	48

nel system, which may have reduced the likelihood of exiting the channel on the ebbing tide. Also, the large number of efficiency fish released on 30 June 2005 may have resulted in “tag collision”, a condition when two or more tags are in the detector field at the same time (Connolly et al. 2008), reducing detection efficiency. Antenna 1 also detected 89 of 92 individuals (97%) that were released outside of the study channel, subsequently entered the channel, and were detected on antenna 2. Following efficiency tests, most efficiency fish (90%) returned to the study channel on subsequent tides (up to 32 days following release), and the system recorded a total of 91 and 224 detections of these fish in 2004 and 2005, respectively. Detections of efficiency fish were not used for other analyses of salmon movements or residence times.

Detection of tagged salmon

In 2004, the PIT detector recorded 493 detections of 123 unique individual tagged salmon that moved into the study channel volitionally after being released elsewhere in the estuary. These individuals included 18% of Chinook salmon tagged and released in the reference marsh (Table 2). In 2005, the system recorded 369 detections of 75 unique fish, 15% of Chinook salmon tagged in the reference marsh but outside the study channel.

During both years, the body size of salmon detected in the study channel was representative of the tagged population. Likelihood of detection and duration over which individuals used the study channel did not appear related to body size when tagged. Likelihood of detection in the study channel was greater for fish captured and tagged at sites above the confluence with the study channel than for those tagged and

released below the confluence (Fig. 4; *G* test with Williams correction used to compare fish tagged above and below the channel, *p* = 0.0014 in 2004 and *p* = 0.0025 in 2005).

Tagged fish were detected between 5 h before and 6 h after high slack tides. Frequency distributions of all detections for both years indicate that peak movement of tagged salmon through the antennas occurred roughly 1 to 2 h before and 3 to 4 h after high slack tides (Fig. 5a). Tagged salmon were detected during both daytime and nighttime tides. Of 862 total detections during both years, roughly half (449 or 52%) occurred between 1 h before sunset and 1 h after sunrise.

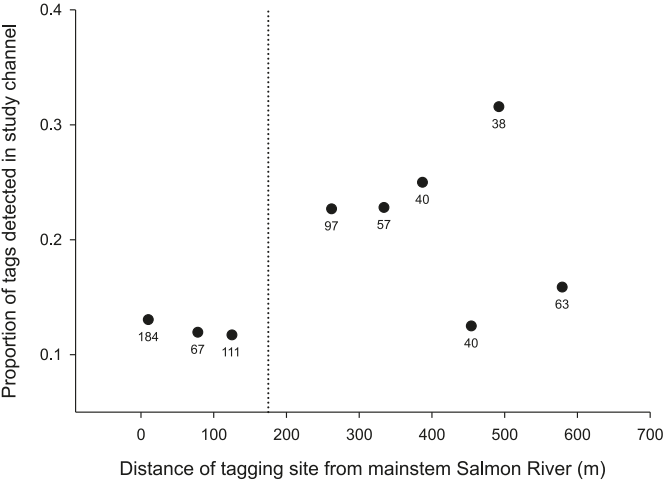
Among all detections at both antennas during 2005, median water depth was significantly shallower when fish were detected during ebb tides than during flood tides (median depth 0.75 m vs. 0.95 m, Wilcoxon rank sum test *p* = 0.0012). Results from 2004, when we did not measure water depth directly, were qualitatively similar. Only 21 (6%) of the total detections in 2005 occurred when water depth was 0.4 m or less, despite the fact that shallow depths made up the greatest proportion of depths recorded at the antenna site (Fig. 6). Of these 21 detections, 17 (81%) occurred during low light conditions between 1 h before sunset and 1 h after sunrise.

Median water temperature at the bottom of the channel when fish were detected was 14.9 °C (interquartile range 13.7 to 16.0 °C) in 2004 and 16.4 °C in 2005 (interquartile range 15.0 to 17.4 °C). High tide water temperature did not appear to limit salmon from using the channel. The warmest temperatures (exceeding 25 °C) occurred during low tides when water was shallow and tagged fish were not moving in the study channel (see Fig. S1 of the supplementary data).<sup>4</sup>

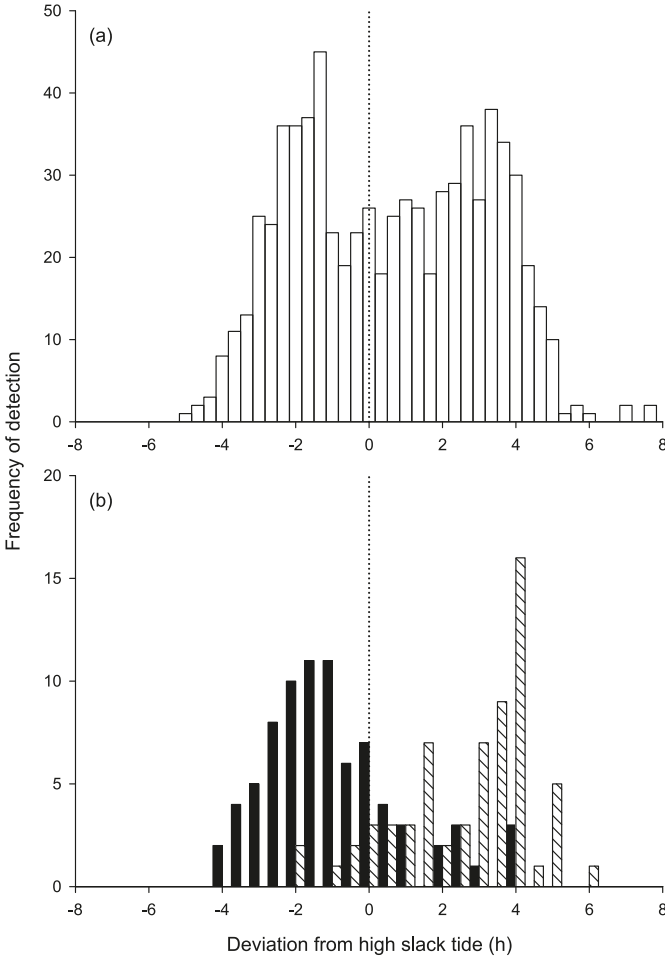
<sup>4</sup>Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5349. For more information on obtaining material refer to <http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html>.

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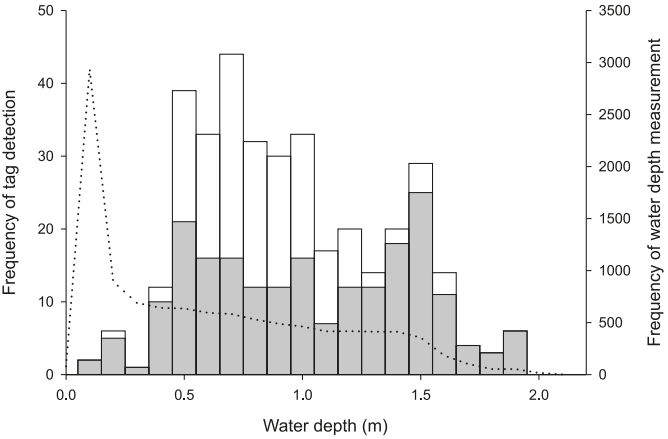
**Fig. 4.** Proportion of individuals detected in the study channel after initial capture at nine tagging sites within the reference marsh channel network. Data are grouped by tagging site and arranged by distance of tagging site from the mainstem Salmon River. Vertical dotted line indicates location of study channel confluence. Sample sizes of fish tagged are indicated for each site.



**Fig. 5.** (a) Frequency of all PIT tag detections at antenna 1, and (b) frequency of fish movements into (solid bars) and out of (hatched bars) the study channel in 2005, relative to the tidal cycle. Vertical dotted lines indicate timing of high slack tide.



**Fig. 6.** Frequency of PIT tag detections by water depth at the detector site in 2005. Shaded portions of bars represent detections that occurred during low light conditions. Dotted line indicates frequency of depth records during the period of time that fish were detected (29 June – 13 September).



**Patterns of movement and residence time of individual salmon**

Most individuals recorded by the PIT tag detector were detected on few occasions — a median of two detections per fish — but several individuals were detected on multiple occasions, including single individuals that were detected up to 44 times in 2004 and 33 times in 2005. Most fish (~65% of those detected) occurred in the study channel during one or two tidal cycles within a few days of tagging and then did not enter the channel again (Fig. 7a). Of the remaining fish, some individuals demonstrated fidelity to the study channel, entering and leaving the channel over multiple successive tidal cycles (as often as 22 tide cycles in a 24-day period) (Fig. 7b). Others were detected on two or more tide cycles separated by several days or weeks without detection, indicating they used the study channel only sporadically during a prolonged period of estuarine residence (Fig. 7c).

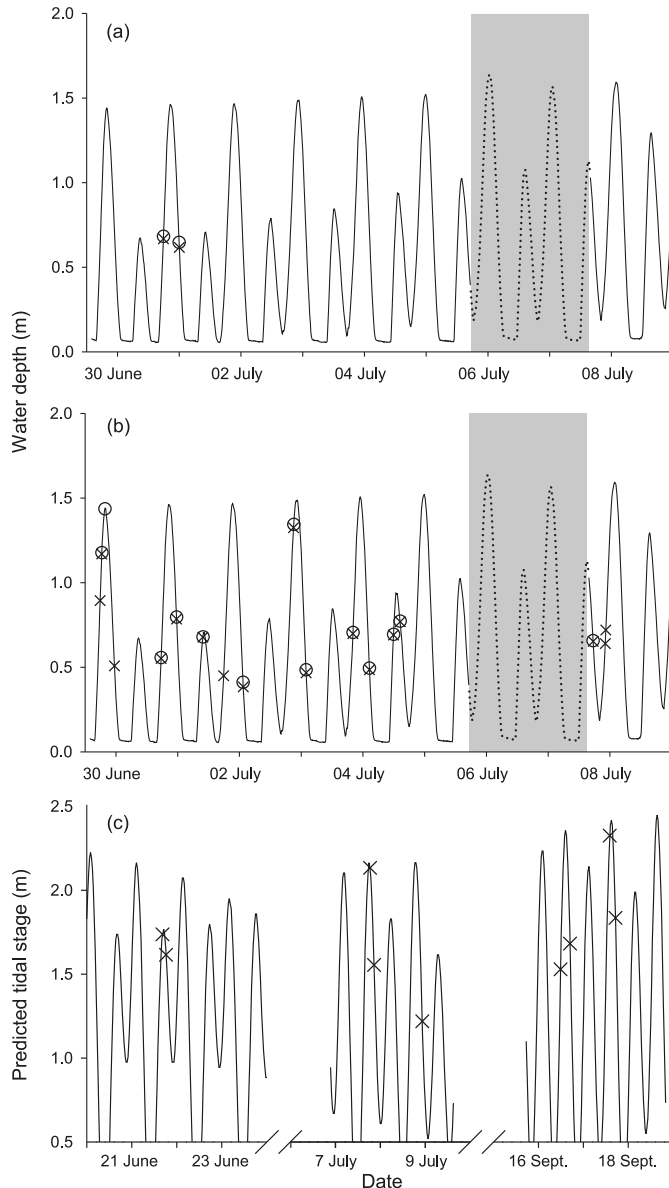
The maximum times-at-large between initial tagging in the reference marsh and final detection in the study channel were 128 days in 2004 and 48 days in 2005. Median times-at-large were 16 days and 9.5 days after tagging in 2004 and 2005, respectively (Table 2).

Using individual detection data from both antennas in 2005, we defined 80 clear entrance movements (individuals detected successively on antenna 1 then antenna 2) and 65 clear exit movements (detected on antenna 2 then antenna 1; Fig. 5b). Most fish moved in the direction of tidal currents: 80% entered during flooding tides and 92% exited on the ebb, 20% entered on the ebb, and 8% exited on the flood. The timing of entrance and exit movements was consistent with periods of peak tag detection before and after high slack tide.

On 57 occasions, individual fish exhibited clear entrance and exit movements during single tidal cycles. Based on these 57 observations (from 36 unique individual fish), the median individual residence time within the channel per tidal cycle was 4.9 h (range 0.37 h to 8.9 h). Residence time showed a weak but significant positive association with tidal magnitude (linear regression of residence time on depth in the channel measured at high slack tide,  $r^2 = 0.16$ ,  $p = 0.002$ ). The longest



**Fig. 7.** Complete detection histories of three individual salmon demonstrate diverse patterns of marsh residence: (a) a typical fish that used the channel on only one tidal cycle after being tagged on 28 June 2005 (85 mm and 7.3 g when tagged); (b) an individual that was tagged on 28 June 2005 (86 mm and 7.3 g) but showed fidelity to the study channel over several tidal cycles; (c) an example of occasional use of the channel by one individual over several months during 2004 (tagged 7 June 2005 at 72 mm and 4.3 g). Detection on antenna 1 is indicated by ×; detection on antenna 2 is indicated by ○ (no antenna 2 in 2004). Continuous lines represent the tidal cycle as water depth at the study site (2005) or predicted tidal stage (2004). (The shaded areas in (a) and (b) indicate a period 5–7 July 2005 when the PIT detector was not operating.)



observed residence times were associated with particularly high tides that occurred at night. On a given tidal cycle, individual fish tended to exit the channel when the water depth was equivalent to or shallower than the depth when they entered. The mean difference in depth between entrance and exit was 20 cm (standard error 5 cm), and water depth at exit

was significantly shallower than depth at entrance (one-sided  $t$  test,  $t_{156} = -3.54$ ,  $p = 0.0004$ ).

## Discussion

Development of FDX PIT tag technology has allowed quantification of individual small fish movement within intertidal salt marsh habitat on the temporal scale of individual tidal cycles. By monitoring movements of PIT-tagged sub-yearling Chinook salmon into and out of a tidal wetland channel, we found evidence that (i) salmon used marsh channel habitat over a broad range of tidal conditions when water depth was greater than 0.4 m; (ii) individual salmon remained in the intertidal channel for a median 4.9 h and as long as 8.9 h per tidal cycle; (iii) the timing of salmon movement into and out of intertidal habitat was not centered on high slack tide, and fish at times swam against tidal currents; (iv) salmon exhibited some fidelity to a specific intertidal channel within the estuarine marsh landscape; and (v) individuals within the population exhibited diverse patterns of residence in the study channel, ranging from hours to months, including periods of continuous and infrequent habitat use.

Although many studies have documented estuary-wide migrations, residence times, and habitat use by juvenile salmonids (e.g., Healey 1980; Kjelson et al. 1982; Miller and Sadro 2003), few have examined the fine-scale movement of individual salmon into and out of shallow marsh habitats as channels drain and fill with each tide (Levy and Northcote 1982). New micro-acoustic tags have been used to study estuarine migration behaviors and survival rates of juvenile salmon (Williams 2008), as well as the fine-scale movements of individuals placed within estuarine habitat enclosures (Semmens 2008). However, such tags are too large for applications involving the small (<90 mm) size classes of salmon that typically reside in wetlands and other shallow estuarine habitats (Levy and Northcote 1982; Simenstad et al. 1982; Bottom et al. 2005b).

Although juvenile salmon usually entered and departed the Salmon River marsh channel in the direction of tidal currents, the asymmetry of salmon movement about high slack water and the high proportion of movements that occurred against ebbing tides indicate that Chinook salmon do not drift passively with the current, but rather enter and actively remain in intertidal habitat until late in the tidal cycle. Peak salmon movement occurred during mid- to late flood tides (i.e., 1–2 h before high slack tide) and late during ebb tides (i.e., 3–4 h after high slack tide). Furthermore, 20% of individuals entered the channel against the ebbing tide, 8% exited against the flooding tide, and fish exited the channel at water depths that were, on average, 20 cm shallower than when they entered. Using trap nets set across marsh channels at high tides, Levy and Northcote (1982) similarly reported that most Chinook salmon and chum salmon (*Oncorhynchus keta*) fry in the Fraser River estuary left intertidal marsh channels during late ebb-tide periods, whereas pink salmon (*Oncorhynchus gorbuscha*) emigrated during early and middle stages of ebbing tides. Pink salmon occur in estuaries at much smaller sizes than Chinook salmon and thus may be less able to maintain position against tidal currents than larger species. Our results for Chinook salmon

differ from patterns observed for nekton in an intertidal creek in South Carolina where most taxa departed the channel at the same depth as they entered (Bretsch and Allen 2006).

Behavioral studies have demonstrated that habitat choices by juvenile salmon involve species-specific tradeoffs between optimal foraging opportunities and predation risks (Magnhagen 1988; Abrahams and Healey 1993) or physiological stresses (Webster et al. 2007). Salt marsh habitats provide productive feeding habitats for juvenile salmon (Levy and Northcote 1982; Simenstad et al. 1982; Shreffler et al. 1992) and have been described as potential predator refugia (Shreffler et al. 1992), but the relative benefits and costs for salmon occupying shallow intertidal marsh channels rarely have been measured (Craig and Crowder 2000). The patterns of salmon residence in the Salmon River study channel may serve to maximize foraging success while limiting predation risks and the bioenergetic costs of increasing water temperatures (Gray 2005). Tagged fish avoided shallow water where avian predation, potential for stranding, and elevated water temperatures may pose increased risks of mortality during receding tides. Occasions when fish were detected in shallow water were usually periods of low light, when risk from visual predators was minimized. Chinook salmon feed actively in Salmon River marsh channels on invertebrate taxa produced within the marsh (Gray et al. 2002). By remaining within the channel as the tide ebbs, individuals may maximize encounters with drifting invertebrate prey exported from the marsh channel network and concentrated during receding tides.

Despite having to vacate tidal channels with each ebb tide, our results indicate that individual salmon may exhibit fidelity at the scale of secondary marsh channels within an intertidal marsh-channel network. For example, some individuals used the study channel repeatedly on successive tides. Moreover, fish tagged in the reference marsh network above the confluence with the study channel were more likely to be detected than those tagged below the confluence. Presumably, this was because fish in the upper portion of the marsh system again penetrated high into the channel network on subsequent tides. Although many individuals that were detected multiple times entered the study channel only sporadically, it is unclear whether such fish were regularly using another, unmonitored area within the reference network. Because the entire population of the intertidal channel network is concentrated within a limited number of subtidal refuge habitats in the mainstem estuary during low tide, some redistribution of individuals within the network likely occurs with each tidal cycle. Consequently, site fidelity may be weaker at finer spatial scales within intertidal channel networks than at coarser scales among networks.

Through continuous monitoring of fish entering and exiting the study channel, our PIT tag methodology discerned considerable variation in the wetland rearing behaviors of individual salmon that may not be apparent from conventional survey methods. For example, some individuals revisited the same small wetland channel intermittently for periods of weeks or months. Conventional methods that use fixed nets to sample periodically (e.g., daily, weekly, or monthly) therefore may greatly underestimate wetland residency and cannot measure variation in the frequencies of ti-

dal excursions among individuals entering and leaving local habitats. The small but noteworthy proportion of tagged Chinook salmon that we observed entering the study channel during ebbing tides would have been excluded from the channel — and thus not included in abundance estimates — by traditional sampling methods that place trap nets across the mouths of tidal channels at high slack tide (e.g., Levy and Northcote 1982; Shreffler et al. 1990; Miller and Simenstad 1997). Such methods also may not detect residence patterns accurately if channels do not drain completely during neap low tides.

Most studies of marsh habitat use by estuarine nekton have sampled during daylight hours (reviewed by Rountree and Able 1993), which may greatly underestimate marsh channel use by animals that are more active or abundant at night (Rountree and Able 2007). Although we did not observe a substantial difference in the number of tagged salmon detected between night and day, the longest tidal residence times of individuals within the marsh occurred during nighttime tides. Passive, in situ tag monitoring did not require additional labor or expense to sample daytime and nighttime tides equally.

Our approach was limited somewhat by the dimensions of the PIT tag antennas available for this research, which required that we artificially narrow the study channel with nets. Improved, unshielded FDX PIT tag antennas measuring approximately 3 m × 0.5 m — about twice the detection area of the antenna used in the present study — since have been tested successfully in salinities of up to 28 PSU (E. Prentice, unpublished). Moreover, the small, shielded antennas that we used likely could detect smaller, 8 mm long FDX PIT tags that are now commercially available, potentially allowing monitoring of even smaller fish. These improvements and the ability to link multiple antennas to a single multiplexing transceiver offer considerable flexibility to span larger channels and to continually monitor the residency and movements of small fish in estuarine habitats.

Human development of coastal areas has altered many estuaries used by salmon (Boulé and Bierly 1987), and in some Oregon estuaries, as much as 80% of former tidal wetland area has become inaccessible to migratory fish as a result of diking, filling, and the installation of tide gates (Good 2000). Wetland restoration projects often attempt to recreate habitats that function equivalently to natural reference sites (Miller and Simenstad 1997; Gray et al. 2002), and fish behaviors, including residence times and movement patterns, have been proposed as important measures of restoration success (Simenstad and Cordell 2000). The fact that most tagged salmon occupied our intertidal study channel only when water reached a minimal depth affirms that restored channels intended as salmon rearing habitat must be designed to maintain sufficient depth during high tides for salmon access. Although higher elevation tidal channels may support and export salmon prey to other areas of the estuary, they likely will not be used by salmon directly.

Based on the timing of movement that we observed, tide gates also are likely to inhibit salmon movement if they remain closed or alter tidal flow at any time during the period beginning roughly 4 h before and ending roughly 6 h after high tide. Thus, although many recent restoration efforts have modified tide gates to improve passage of adult and ju-



venile fish (Giannico and Souder 2004), it is likely that any gate that functions to limit tidal flooding (the fundamental purpose of tide gates) will negatively affect access to habitat by juvenile salmon. The small proportion of tagged fish that entered our channel during the ebbing tide, however, suggests that salmon may opportunistically access habitats above tide gates if gates open early enough and remain open for a sufficient period during ebb tides.

Bottom et al. (2005a) provided evidence that restoration of marsh habitat in the Salmon River estuary has expanded expression of estuarine-rearing life histories within the contemporary Chinook salmon population. Juvenile Chinook salmon now enter the ocean at a broader range of sizes and times compared with a period prior to marsh restoration. Such behavioral diversity may spread the risks posed by variable oceanic or climatic conditions and increase resilience of the salmon population. The individual-based approach in this study reveals on a fine scale the ways in which juvenile Chinook interact with and exploit intertidal wetland habitat and affirms that a diversity of marsh rearing patterns exists in the present Chinook salmon population. The behavior of individuals on this finer scale is the mechanism that leads to the population-scale responses to restored habitat structure observed by Bottom et al. (2005a).

Preserving connectivity of intertidal marsh habitats within the estuary is critical to maintaining expression of behavioral diversity in estuarine rearing salmon. We suggest that future marsh rearing studies incorporate multiple PIT detection sites to examine the patterns of habitat use by individuals across the estuarine landscape and the connections among habitats that support diverse salmon rearing and migration behaviors.

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## References

Abrahams, M.V., and Healey, M.C. 1993. A comparison of the willingness of four species of Pacific salmon to risk exposure to a predator. *Oikos*, **66**(3): 439–446. doi:10.2307/3544938.

Adams, A.J., Wolfe, R.K., Pine, W.E., and Thornton, B.L. 2006. Efficacy of PIT tags and an autonomous antenna system to study the juvenile life stage of an estuarine-dependent fish. *Estuaries Coasts*, **29**(2): 311–317. doi:10.1007/BF02781999.

Bottom, D.L., Jones, K.K., Cornwell, T.J., Gray, A., and Simenstad, C.A. 2005a. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). *Estuar. Coast. Shelf Sci.* **64**(1): 79–93. doi:10.1016/j.ecss.2005.02.008.

Bottom, D.L., Simenstad, C.A., Burke, J., Baptista, A.M., Jay, D.A., Jones, K.K., Casillas, E., and Schiewe, M.H. 2005b. Salmon at river's end: the role of the estuary in the decline and re-

covery of Columbia River salmon. US Dep. Comm., NOAA Tech. Memo. NMFS-NWFSC-68.

Boulé, M. E., and K. F. Bierly. 1987. History of wetland development and alteration: what have we wrought? *Northwest Environ. J.* **3**(1): 43–61.

Bretsch, K., and Allen, D.M. 2006. Tidal migrations of nekton in salt marsh intertidal creeks. *Estuaries Coasts*, **29**(3): 474–486.

Brown, R.S., Geist, D.R., Deters, K.A., and Grassell, A. 2006. Effects of surgically implanted acoustic transmitters >2% of body mass on the swimming performance, survival and growth of juvenile sockeye and Chinook salmon. *J. Fish Biol.* **69**(6): 1626–1638. doi:10.1111/j.1095-8649.2006.01227.x.

Congleton, J.L., Davis, S.K., and Foley, S.R. 1981. Distribution, abundance, and outmigration timing of chum and chinook salmon fry in the Skagit salt marsh. In *Salmon and Trout Migratory Symposium*. Edited by E.L. Brannon and E.O. Salo. University of Washington Press, Seattle, Washington. pp. 153–163.

Connolly, P.J., Jezorek, I.G., Martens, K.D., and Prentice, E.F. 2008. Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. *N. Am. J. Fish. Manage.* **28**(2): 402–417. doi:10.1577/M07-008.1.

Craig, J.K., and Crowder, L.B. 2000. Factors influencing habitat selection in fishes with a review of marsh ecosystems. In *Concepts and controversies in tidal marsh ecology*. Edited by M.P. Weinstein and D.A. Kreeger. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 241–266.

Giannico, G.R., and Souder, J.A. 2004. The effects of tidegates on estuarine habitats and migratory fish. Oregon Sea Grant, Oregon State University, Corvallis, Oregon, Report No. ORESU-G-04-002.

Gibson, R.N. 2003. Go with the flow: tidal migrations in marine animals. *Hydrobiologia*, **503**(1–3): 153–161. doi:10.1023/B:HYDR.0000008488.33614.62.

Good, J.W. 2000. Summary and current status of Oregon's estuarine ecosystems. In *The Oregon State of the Environment Report 2000*. Oregon Progress Board, Salem, Oregon.

Gray, A. 2005. The Salmon River estuary: restoring tidal inundation and tracking ecosystem response. Ph.D. dissertation, University of Washington, Seattle, Washington.

Gray, A., Simenstad, C.A., Bottom, D.L., and Cornwell, T.J. 2002. Contrasting functional performance of juvenile salmon habitat in recovering wetlands of the Salmon River estuary, Oregon, USA. *Restor. Ecol.* **10**(3): 514–526. doi:10.1046/j.1526-100X.2002.01039.x.

Healey, M.C. 1980. Utilization of the Nanaimo River estuary by juvenile chinook salmon, *Oncorhynchus tshawytscha*. *Fish. Bull. (Washington, D.C.)*, **77**: 653–668.

Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In *Pacific salmon life histories*. Edited by C. Groot and L. Margolis. UBC Press, Vancouver, British Columbia, Canada. pp. 313–393.

Jefferson, C.A. 1974. Plant communities and succession in Oregon coastal salt marshes. Ph.D. dissertation, Oregon State University, Corvallis, Oregon.

Kjelson, M.A., Raquel, P.F., and Fisher, F.W. 1982. Life history of fall-run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento–San Joaquin estuary, California. In *Estuarine comparisons*. Edited by V.S. Kennedy. Academic Press, New York. pp. 393–411.

Levy, D.A., and Northcote, T.G. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. *Can. J. Fish. Aquat. Sci.* **39**(2): 270–276. doi:10.1139/f82-038.

- Magnhagen, C. 1988. Predation risk and foraging in juvenile pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). *Can. J. Fish. Aquat. Sci.* **45**(4): 592–596. doi:10.1139/f88-072.
- McCormick, M.I., and Smith, S. 2004. Efficacy of passive integrated transponder tags to determine spawning-site visitations by a tropical fish. *Coral Reefs*, **23**: 570–577.
- Meynecke, J.-O., Poole, G.C., Werry, J., and Lee, S.Y. 2008. Use of PIT tag and underwater video recording in assessing estuarine fish movement in a high intertidal mangrove and salt marsh creek. *Estuar. Coast. Shelf Sci.* **79**(1): 168–178. doi:10.1016/j.ecss.2008.03.019.
- Miller, B.A., and Sadro, S. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Trans. Am. Fish. Soc.* **132**(3): 546–559. doi:10.1577/1548-8659(2003)132<0546:RTASMO>2.0.CO;2.
- Miller, J.A., and Simenstad, C.A. 1997. A comparative assessment of a natural and created estuarine slough as rearing habitat for juvenile chinook and coho salmon. *Estuaries*, **20**(4): 792–806. doi:10.2307/1352252.
- Moser, M.L., Olson, A.F., and Quinn, T.P. 1991. Riverine and estuarine migratory behavior of coho salmon (*Oncorhynchus kisutch*) smolts. *Can. J. Fish. Aquat. Sci.* **48**(9): 1670–1678. doi:10.1139/f91-198.
- Muir, W.D., Smith, S.G., Williams, J.G., Hockersmith, E.E., and Skalski, J.R. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993–1998. *N. Am. J. Fish. Manage.* **21**(2): 269–282. doi:10.1577/1548-8675(2001)021<0269:SEFMYC>2.0.CO;2.
- Newby, N.C., Binder, T.R., and Stevens, E.D. 2007. Passive integrated transponder (PIT) tagging did not negatively affect the short-term feeding behavior or swimming performance of juvenile rainbow trout. *Trans. Am. Fish. Soc.* **136**(2): 341–345. doi:10.1577/T06-110.1.
- Ombredane, D., Bagliniere, J.L., and Marchand, F. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (*Salmo trutta* L.) and their use for studying movement in a small river. *Hydrobiologia*, **371–372**: 99–106. doi:10.1023/A:1017022026937.
- Prentice, E.F., Flagg, T.A., McCutcheon, C.S., and Cross, D.C. 1990a. Equipment, methods, and an automated data-entry station for PIT tagging. *Am. Fish. Soc. Symp.* **7**: 334–340.
- Prentice, E.F., Flagg, T.A., and McCutcheon, S. 1990b. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *Am. Fish. Soc. Symp.* **7**: 317–322.
- Rountree, R.A., and Able, K.W. 1993. Diel variation in decapod crustacean and fish assemblages in New Jersey polyhaline marsh creeks. *Estuar. Coast. Shelf Sci.* **37**(2): 181–201. doi:10.1006/ecss.1993.1050.
- Rountree, R.A., and Able, K.W. 2007. Spatial and temporal habitat use patterns for saltmarsh nekton: implications for ecological functions. *Aquat. Ecol.* **41**(1): 25–45. doi:10.1007/s10452-006-9052-4.
- Rozas, L.P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries*, **18**(4): 579–590. doi:10.2307/1352378.
- Schreck, C.B., Stahl, T.P., Davis, L.E., Roby, D.D., and Clemens, B.J. 2006. Mortality estimates of juvenile spring–summer Chinook salmon in the Lower Columbia River and estuary 1992–1998: evidence for delayed mortality? *Trans. Am. Fish. Soc.* **135**(2): 457–475. doi:10.1577/T05-184.1.
- Semmens, B.X. 2008. Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary. *Can. J. Fish. Aquat. Sci.* **65**(9): 2053–2062. doi:10.1139/F08-107.
- Shreffler, D.K., Simenstad, C.A., and Thom, R.M. 1990. Temporary residence by juvenile salmon in a restored estuarine wetland. *Can. J. Fish. Aquat. Sci.* **47**(11): 2079–2084. doi:10.1139/f90-232.
- Shreffler, D.K., Simenstad, C.A., and Thom, R.M. 1992. Foraging by juvenile salmon in a restored estuarine wetland. *Estuaries*, **15**(2): 204–213. doi:10.2307/1352693.
- Simenstad, C.A. 1983. The ecology of estuarine channels of the Pacific Northwest coast: a community profile. US Fish and Wildlife Service Report No. FWS/OBS-83/05.
- Simenstad, C.A., and Cordell, J.R. 2000. Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific Northwest estuaries. *Ecol. Eng.* **15**(3–4): 283–302. doi:10.1016/S0925-8574(00)00082-3.
- Simenstad, C.A., Fresh, K.L., and Salo, E.O. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. *In* *Estuarine comparisons*. Edited by V.S. Kennedy. Academic Press, New York. pp. 343–364.
- Webster, S.J., Dill, L.M., and Korstrom, J.S. 2007. The effects of depth and salinity on juvenile Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) habitat choice in an artificial estuary. *J. Fish Biol.* **71**(3): 842–851. doi:10.1111/j.1095-8649.2007.01553.x.
- Williams, J.G. 2008. Mitigating the effects of high-head dams on the Columbia River, USA: experience from the trenches. *Hydrobiologia*, **609**(1): 241–251. doi:10.1007/s10750-008-9411-3.
- Zydlewski, G.B., Horton, G., Dubreuil, T., Letcher, B., Casey, S., and Zydlewski, J. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. *Fisheries*, **31**(10): 492–502. doi:10.1577/1548-8446(2006)31[492:RMOFIS]2.0.CO;2.